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THE SUSCEPTIBILITY OF PERENNIAL DELPHINIUMS TO SIX VIRUSES¹

HENRY H. P. SEVERIN²

PERENNIAL DELPHINIUMS (hybrid and horticultural varieties of several species of *Delphinium*) have been found to be naturally infected with several virus diseases. Three such diseases—California aster yellows, celery calico, and delphinium ringspot—have been reported in previous papers (5, 6, 7).³ A fourth—tomato spotted wilt—is reported in this paper. Also, included herein are the results of experimental infection of delphiniums with five other viruses—common cucumber mosaic,⁴ western cucumber mosaic, tobacco ringspot, ordinary tobacco mosaic, and curly top. None of these five has been found on delphinium in California under natural conditions up to the present time, but the first has been reported by other investigators to occur naturally on this host plant in England.

TOMATO SPOTTED WILT

Spotted wilt on perennial delphinium has been reported in California by Gardner, Tompkins, and Whipple (2). Smith (8, 9) reported that considerable damage may be caused to delphinium by the spotted-wilt virus in England and he described the symptoms of the disease as follows: black rings, or numerous double concentric rings, or patches of dead tissue appear on the older leaves. The younger leaves are malformed with edges yellow, necrotic, and inwardly curled. Necrotic patches may develop on the stems and older leaves.

Spotted wilt ranks next to aster yellows (6) in seriousness as a disease of delphinium in the coastal regions of California. Entire fields of delphiniums have been observed to be infected with spotted wilt near San Leandro, San Bruno, and Berkeley.

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² Associate Entomologist in the Experiment Station.

³ Italic figures in parentheses refer to "Literature Cited" at the end of this paper.

⁴ Common-cucumber-mosaic, tobacco-ringspot, and ordinary-tobacco-mosaic viruses were kindly sent to me by James Johnson, University of Wisconsin.

Numerous efforts have been made to infect experimentally by mechanical inoculation (4) varieties of delphinium seedlings and two-year-old delphiniums with the spotted-wilt virus; but all attempts using naturally infected tomatoes, garden nasturtium (*Tropaeolum majus*), and bull mallow (*Malva niceensis*) as a source of virus were failures. On the other hand, when the virus extract from calla (*Zantedeschia aethiopica*) was inoculated in delphiniums, infections were occasionally obtained.

The early symptoms of spotted wilt on delphinium are variable and are often difficult to distinguish from delphinium calico, but the late symptoms of the disease are constant and reliable. The first symptom that appears on the leaves of experimentally infected delphiniums is pale green, circular, elliptical, or irregular areas (plate 1, A), which later may become surrounded by chlorotic rings (plate 1, B). Some leaves may show numerous, double, concentric rings of various sizes, each composed of an outer green and inner chlorotic ring (plate 1, C) or a chlorotic ring (plate 1, D) surrounding a green center. Sometimes both rings are so small that the inner ring encloses a pinpoint green center. Large lemon-yellow blotches with or without rings sometimes extend into the lobes of the leaves or pale-green areas are embedded in the yellow tissue. Sometimes within the yellow areas, green or chlorotic banding of the veins occurs (plate 1, E). The margin of the leaves may be lemon yellow, and often irregular, chlorotic areas extend toward the base of the lobes (plate 1, F).

In the later stages of the disease, black rings of various sizes, often irregular in shape, surround chlorotic tissue (plate 2, A) which later becomes black on the lower leaves (plate 2, B). Black patches often spread over most of the lobes of the leaves (plate 2, C, D), and the petioles and veins may become necrotic (plate 2, E). The lower leaves turn brown and become dry (plate 2, F) with the blackened areas still conspicuous. As the disease progresses, the intermediate and upper leaves develop the ring, the chlorotic, and later the black pattern. The flowers on infected plants were normal.

During the early spring the ring, the chlorotic, and the black patterns appeared on the lower leaves of the new shoots after attaining a height of from 1 to 2 feet and progressively on the intermediate and upper leaves. After the old stock was cut off, the successive symptoms of the disease again appeared on the new shoots during the summer. No symptoms appeared on the leaves of marked infected delphiniums during the past mild winter (1941-42). These observations were made on two- and three-year-old Pacific-strain delphiniums grown in my home garden during 1939 to 1941.

Numerous attempts have been made to recover the spotted-wilt virus from naturally infected delphiniums and transfer it by mechanical inoculation to healthy delphiniums, Marglobe tomatoes, *Nicotiana glutinosa*, Turkish tobacco, Jimsonweed (*Datura Stramonium*) and asters, without results. If the onion thrips (*Thrips tabaci* Lindeman) or *Frankliniella occidentalis* (Perg.) had been used as vectors of the virus, instead of mechanical inoculation, the virus might have been recovered from naturally infected delphiniums.

Celery calico (5) was sometimes recovered from delphiniums infected with spotted wilt.

COMMON CUCUMBER MOSAIC

On Delphiniums.—According to Smith (8, 9), delphinium is very susceptible to and frequently infected with cucumber-mosaic virus in England; he describes the symptoms as follows: "Affected plants present a yellowish (chlorotic) appearance and there are pale areas on the leaves following the veins. A rather faint green mosaic mottle is usually present. As a rule diseased plants are stunted in comparison with healthy plants and the flowers are poor and few in number."

In perennial delphiniums grown from seeds and experimentally infected with common cucumber mosaic by mechanical inoculation (4), a considerable amount of variation occurred in the development of symptoms of the disease in different varieties and hybrids, and even in different plants of the same variety or hybrid. The first symptom which frequently appeared on some of the younger leaves was circular, chlorotic areas (plate 3, A), sometimes distributed along the veins (plate 4, A), which coalesced and formed pale-yellow vein banding (plate 4, B), and later chlorosis sometimes spread in all of the lobes of the leaf (plate 4, C, D). A common symptom on some of the lower leaves was green spotting in the chlorotic areas in one or more lobes of a leaf (plate 3, C). Green vein banding occurred on some leaves of an infected plant (plate 3, E). Sometimes a faint mottling or mosaic pattern (plate 4, E) appeared on one or more leaves of a plant. The symptoms described were infrequently accompanied with crinkling, puckering, and distortion (plate 4, F). Green blisterlike elevations, which are a common symptom of cucumber mosaic on many host plants, were rare on the leaves of infected delphiniums (plate 4, F). The prevailing discoloration, if it occurred, was lemon yellow; but in some delphinium varieties or hybrids, the margin of the leaf was orange, fading to pale yellow within the lobes. All delphiniums observed were kept until the blossoming period; but, without exception, the flowers were normal.

TABLE 1

LIST OF DELphinium VARIETIES AND HYBRID SEEDLINGS EXPERIMENTALLY INFECTED
WITH COMMON CUCUMBER MOSAIC, INCUBATION PERIOD OF
DISEASE, AND RECOVERY OF VIRUS

Delphinium variety or hybrid and date inoculated (1939-40)	Delphinium inoculated	Delphiniums infected	Incubation period of disease in plants		Recovery of virus from infected delphiniums	
			Range	Mean	Cucumbers inoculated	Cucumbers infected
Blackmore and Langdon hybrids:						
October 31.....	5	2	28-55	41.5	10	0
Belladonna tall hybrids:						
July 9.....	5	1	7		5	0
August 14.....	5	3	43-57	47.7	15	15
Chinese Azure Blue:						
August 31.....	5	1	40	5	0
Clivenden Beauty:						
July 8.....	5	2	6-22	11.0	10	0
September 17.....	5	2	54-54	54.0	10	10
Delphinium Parryi var. maritimum:						
November 15.....	2	1	—*	—*	5	1
Dreer's De Luxe Art shades:						
July 9.....	5	1	9	5	1
Dreer's De Luxe Dark-Blue shades:						
July 9.....	5	1	8		5	2
September 17.....	2	2	45-54	49.5	10	10
Dreer's De Luxe Light-Blue shades:						
July 9.....	1	1	—*	—*	5	5
August 31.....	4	3	25-26	25.7	15	0
English hybrids Deep-Blue shades:						
July 9.....	5	1	22	5	5
Burpee's Floradale Giants Deep Blue:						
July 9.....	1	1	—*	—*	5	4
August 31.....	5	1	40	5	0
Burpee's Floradale Giants Light Blue:						
July 9.....	1	1	—*	—*	5	5
Burpee's Floradale Giants Mid Blue:						
July 9.....	3	2	22-24		10	5
August 31.....	2	2	38-38	38.0	10	10
September 17.....	1	1	34	5	5
A. & M. Gold Medal hybrid:						
July 8.....	4	2	7-10	8.5	10	10
Gold Medal hybrids:						
September 17.....	1	1	55	5	5
Hardy larkspur (<i>Delphinium formosum</i>):						
September 17.....	5	2	27-53	45.0	10	10
Iceberg:						
August 31.....	5	2	25-26	25.5	10	4
September 17.....	1	1	24	5	5
Lemon Gem:						
July 9.....	3	3	—*	—*	15	15
Burpee's Mammoth hybrids:						
July 9.....	5	2	6-7	6.5	10	0
Pacific Giant mixed:						
July 9.....	5	2	6-20	13.0	10	0
September 17.....	1	1	38	5	5
Pacific Giant White:						
July 8.....	5	5	—*	—*	25	25
A. & M. Sunbeam hybrids:						
July 9.....	4	4	5-24	11.2	20	12
Total.....	106	54	270	169
Percentage.....	50.9	62.9

* No symptoms, but virus recovered from infected delphiniums.

The type of infection was systemic. The symptoms sometimes appeared on the inoculated leaves of delphinium seedlings, or on a few of the intermediate or upper leaves not inoculated. The virus was recovered and transferred to White Spine cucumber plants, from the inoculated leaves, and also from the intermediate and upper leaves not inoculated.

The delphinium varieties experimentally infected with the virus are listed in table 1. Of a total of 106 delphinium seedlings inoculated, 54, or 50.9 per cent, were infected. The virus was recovered from 39 of 54 infected delphiniums, or 72.2 per cent; the infected plants included 12 symptomless carriers.

On Cucumbers.—The first symptom of common cucumber mosaic on the cotyledons of White Spine cucumber seedlings is chlorotic rings, each enclosing a green area. Sometimes an outer chlorotic ring and an inner green ring surround a chlorotic area. Later the green area becomes chlorotic and a pinpoint necrotic center appears. Cleared veinlets develop on the first leaf when small (plate 5, A), later numerous rings appear similar to those on the cotyledons but much smaller. The blade is often cupped inward along the midrib, or the margin is rolled outward and the petiole bent downward (plate 5, B). The second leaf is sometimes balled (plate 5, B). Blisterlike elevations develop on some of the younger leaves. In a later stage, chlorosis begins at the margin of the first leaf and sometimes progresses until the entire blade becomes yellow. The older leaves are mottled with yellow or orange and green areas. Necrotic streaks which crack later appear on the stem and on some of the petioles, and finally the stem may collapse and the plant die.

WESTERN CUCUMBER MOSAIC

The present known distribution of western cucumber mosaic is in the interior regions of California; the disease is common in the Sacramento and San Joaquin valleys, but no infected host plants have been found in the coastal regions of the San Francisco Bay district, Santa Clara Valley, or in the fog belt of the Salinas Valley. The host range, property studies, and vectors of this virus are the subjects of a separate study.

Since western-cucumber-mosaic virus produces fern leaf, filiform leaf, or shoestring leaf on tomato and other host plants, an examination was made of a large number of delphiniums in the central-coastal district that had such malformed leaves (fig. 1) and dwarfed and frequently brown and dried flowers (fig. 2, A, B). All attempts to recover from these delphiniums a virus producing such symptoms on tomato and other host plants were failures. California-aster-yellows and celery-calico viruses were recovered from delphiniums with malformed leaves and

abnormal flowers, but these viruses do not produce such symptoms on delphinium. No intensive investigation of western cucumber mosaic on delphinium in the interior regions of California has been made.

In perennial delphiniums grown from seeds experimentally infected with western cucumber mosaic by mechanical inoculation (4), the symp-

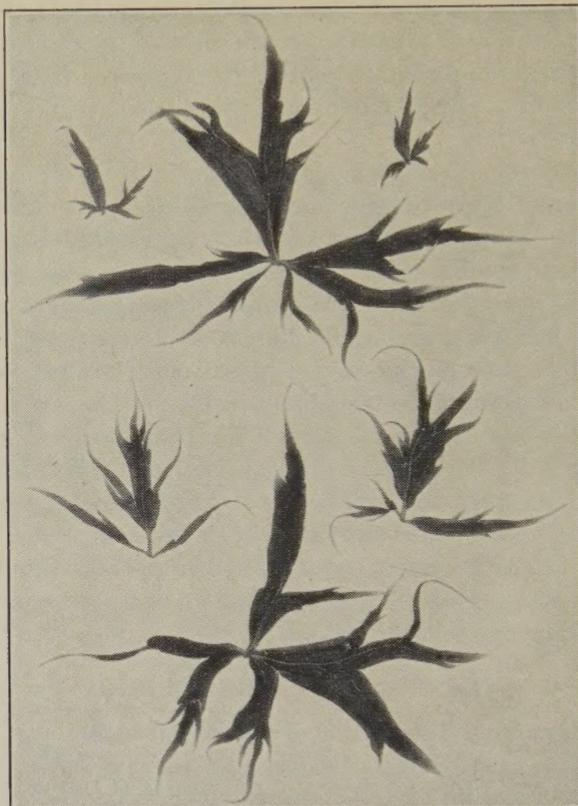


Fig. 1.—Malformed leaves resembling fern leaf, filiform leaf, or shoestring leaf (cause unknown) on Dreer's De Luxe delphinium. The virus of celery calico was recovered from this plant and transferred to cucumbers and Turkish tobacco, but this virus does not produce the symptom. (Mt. Eden, December 22, 1938.)

toms on the leaves are somewhat milder than those of common cucumber mosaic. They are usually not conspicuous and may be limited to one or more inoculated leaves or to a few of the intermediate or upper leaves not inoculated. Some infected delphinium varieties or hybrids show a pale, yellow discoloration of a few leaves. Plate 3 shows a comparison of some of the symptoms caused by common and by western cucumber mosaic:

circular or elongated, chlorotic areas are illustrated in *A*, *B*; green spotting in chlorotic areas in *C*, *D*; and green vein banding in *E*, *F*. The flowers were normal with both viruses.

The type of infection was systemic as determined by the development of symptoms of the disease and recovery of the virus as described for common cucumber mosaic.



Fig. 2.—Spikes of Dreer's De Luxe delphinium showing fern leaf, filiform leaf, or shoestring leaf (cause unknown): *A*, spike showing dwarfed flowers and seed pods; *B*, spike showing brown and dried flowers. (Mt. Eden, December 27, 1938.)

The delphinium varieties and hybrids experimentally infected with the virus are listed in table 2. Of a total of 197 delphiniums inoculated, 127, or 64.0 per cent, were infected. The virus was recovered from 125 of 127 infected delphiniums, or 98.4 per cent; the infected plants included 75 symptomless carriers.

The incubation period of the disease varied from 6 to 55 days, as shown in table 2.

The virus was recovered from experimentally infected delphiniums

TABLE 2
LIST OF DELphinium VARIETIES AND HYBRID SEEDLINGS EXPERIMENTALLY INFECTED
WITH WESTERN CUCUMBER MOSAIC, INCUBATION PERIOD OF
DISEASE, AND RECOVERY OF VIRUS

Delphinium variety or hybrid and date inoculated (1939-40)	Delphiniums inoculated	Delphiniums infected	Incubation period of disease in plants		Recovery of virus from infected delphiniums	
			Range	Mean	Cucumbers inoculated	Cucumbers infected
					number	number
Blackmore and Langdon Giants:						
June 28.....	1	1	15*	5	0
January 16.....	3	3	—*	—*	15	15
Belladonna tall hybrids:						
June 28.....	5	1	13	5	0
Chinese Azure Blue:						
July 8.....	3	3	—*	—*	15	15
Chinese Dark Blue:						
June 25.....	5	1	19	5	5
December 20.....	3	3	—*	—*	15	9
October 1.....	1	1	—*	—*	5	5
December 20.....	3	1	—*	—*	5	3
Clivenden Beauty:						
November 20.....	5	5	—*	—*	25	25
A. & M. Clivenden Beauty:						
June 25.....	5	4	11-12	11.5	20	20
<i>Delphinium cardinale</i> :						
June 2.....	3	3	—*	—*	15	9
<i>Delphinium grandiflorum</i> var. <i>album</i> :						
June 25.....	5	3	19-34	24.0	15	15
<i>Delphinium Zazil</i> :						
March 14.....	1	1	—*	—*	5	5
Dreer's De Luxe Art shades:						
June 28.....	5	4	8-17	14.0	20	20
Dreer's De Luxe Dark-Blue shades:						
June 28.....	5	2	14-16	15.0	10	10
November 19.....	4	4	—*	—*	20	20
Dreer's De Luxe Light-Blue shades:						
July 8.....	1	1	—*	—*	5	1
Dreer's De Luxe Mid-Blue shades:						
June 28.....	5	3	8-15	11.0	15	15
November 19.....	5	1	—*	—*	5	5
Dwarf Chinese Blue Butterfly:						
June 28.....	5	2	15-39	27.0	10	10
English Hybrids Deep-Blue shades:						
June 28.....	5	1	14	5	4
English Hybrids Light-Blue shades:						
July 8.....	1	1	9	5	2
English Hybrids Mid-Blue shades:						
June 25.....	5	3	18-20	19.0	15	15
November 19.....	5	1	—*	—*	5	5
English Hybrids Pastel shades:						
July 8.....	2	2	—*	—*	10	10
August 31.....	5	1	55	5	5
Burpee's Floradale Giants Deep Blue:						
July 8.....	1	1	—*	—*	5	5
Carried forward.....	87	57	285	253

* No symptoms, but virus recovered from infected delphiniums.

TABLE 2—Concluded

Delphinium variety or hybrid and date inoculated (1939-40)	Delphiniums inoculated	Delphiniums infected	Incubation period of disease in plants		Recovery of virus from infected delphiniums	
			Range	Mean	Cucumbers inoculated	Cucumbers infected
	number	number	days	days	number	number
Brought forward.....	97	57	285	253
Burpee's Floradale Giants Light Blue:						
July 8.....	2	2	—*	—*	10	2
August 31.....	1	1	35	5	5
Burpee's Floradale Giants Mid Blue:						
August 31.....	5	3	35-35	35.0	15	15
Giant Single and Double hybrids:						
July 8.....	4	4	—*	—*	20	8
A. & M. Gold Medal hybrids:						
June 25.....	5	2	15-19	17.0	10	10
Gold Medal hybrids:						
July 8.....	3	3	—*	—*	15	15
Hardy larkspur (<i>Delphinium formosum</i>):						
June 25.....	5	4	11-11	11.0	20	20
October 1.....	5	5	—*	—*	25	25
Hybrida mixed:						
June 25.....	5	4	11-22	16.2	20	20
November 20.....	5	4	—*	—*	20	20
Iceberg:						
June 28.....	5	1	9	5	5
August 31.....	5	3	35-35	35.0	15	15
Improved Belladonna:						
November 19.....	5	5	—*	—*	25	16
Improved English hybrids mixed:						
July 8.....	1	1	—*	—*	5	5
Lady Guinevere:						
November 20.....	5	5	—*	—*	25	25
Lemon Gem:						
November 20.....	5	5	—*	—*	25	25
Burpee's Mammoth hybrids:						
July 8.....	4	1	6	5	5
July 8.....	2	2	—*	—*	10	10
October 1.....	1	1	—*	—*	5	5
New Hollyhock strain:						
November 20.....	5	5	—*	—*	25	25
Pacific Giant mixed:						
June 28.....	5	3	15-17	12.3	15	9
Pacific Giant White:						
June 25.....	5	2	15-18	16.5	10	10
A. & M. Sunbeam hybrids:						
July 8.....	5	1	7	5	5
July 8.....	2	2	—*	—*	10	8
Wrexham Hollyhock strain:						
October 1.....	5	1	—*	—*	5	5
Total.....	197	127	665	550
Percentage.....	64.0	82.7

* No symptoms, but virus recovered from infected delphiniums.

and transferred to White Spine cucumber by mechanical inoculation. The first symptom of western cucumber mosaic on the cotyledons of cucumber seedlings is chlorotic rings, each surrounding a green area, which later becomes necrotic. The first leaf is often cupped inward along the midrib and with the margin rolled inward, but later the blade may expand normally. Numerous, small, circular, chlorotic areas appear on the first leaf (plate 5, C) and these coalesce later (plate 5, D). Necrosis of the circular, chlorotic areas may occur about 1 month after inoculation. Some of the younger leaves may show blisterlike elevations. The older leaves are sometimes malformed and become mottled with yellow and green areas. No necrosis of the stem and petioles occurs, western cucumber mosaic differing in this respect from ordinary cucumber mosaic.

TOBACCO RINGSPOT

Wingard (10) experimentally infected 62 species of plants belonging to 38 genera in 17 families with tobacco-ringspot virus but made no attempt to infect any species of the family Ranunculaceae, to which delphinium belongs.

Twenty-five perennial delphinium seedlings were mechanically inoculated (4) with tobacco-ringspot virus, and 4 plants developed symptoms of the disease. Five Pacific-strain two-year-old delphiniums were inoculated and reinoculated with the virus but failed to show symptoms.

The ringspots were composed of alternating, concentric, chlorotic and green rings surrounding green or chlorotic tissue in the center (plate 6, A). The ringspots varied considerably in number and size on the leaves (plate 6, B).

The type of infection was systemic. On delphinium seedlings, ringspots appeared on the newly developing basal leaves that were not inoculated and on the lower leaves of the stalk but appeared only faintly on the intermediate leaves and finally failed to appear on the upper or younger leaves.

The virus was recovered from delphinium leaves showing ringspots and from the upper leaves not showing symptoms when the expressed juice was inoculated in White Spine cucumbers. The first symptom of tobacco ringspot on the cotyledons of cucumber seedlings is numerous, pale, chlorotic rings, each enclosing a green area. The green area gradually becomes smaller, the chlorotic ring widens, until the entire circular area becomes chlorotic. A pinpoint necrotic center appears in the chlorotic area and later enlarges until the entire circular area becomes necrotic.

The sequence of symptoms on the first leaf is somewhat similar to

that on the cotyledons. The chlorotic rings surrounding green areas are smaller and more numerous (plate 5, E) than on the cotyledons. Frequently the chlorotic areas are bounded by cleared veinlets (plate 5, E). In the later stage a chlorotic ring surrounds necrotic tissue (plate 5, F), which sometimes drops out, leaving a hole.

The second leaf is usually cupped inward along the midrib, with rolled margin, and the blade becomes puckered with circular chlorotic areas.

ORDINARY TOBACCO MOSAIC

Grant (3) infected an annual larkspur (*Delphinium Consolida*) with the tobacco-mosaic virus; the symptom expression was stunting of the plants, mottling, yellowing, and necrosis. The type of infection was systemic.

Blackmore and Langdon and Pacific-strain perennial delphiniums experimentally infected with tobacco mosaic by mechanical inoculation (4) frequently showed brown necrotic streaks along the veins of the inoculated leaves (plate 6, C) and large intervenal necrotic areas (plate 6, D), followed by yellowing and drying of the leaves.

The type of infection was local and not systemic. In twenty-five delphinium seedlings inoculated with the tobacco-mosaic virus, symptoms of the disease developed only on the inoculated leaves. The virus was recovered and transferred to *Nicotiana glutinosa* from the inoculated leaves but not from the newly developing leaves. In another experiment two-year-old Pacific-strain delphiniums were inoculated with the ordinary-tobacco-mosaic virus, a few of the upper or youngest, the intermediate, and the lowest or basal leaves being inoculated on each plant. The inoculated leaves were marked by cutting off the tip of a lobe. The virus was recovered 17 days after inoculation only from the inoculated leaves. The flowers were normal.

The virus was recovered from infected leaves of delphiniums and transferred to *Nicotiana glutinosa*, which developed local lesions (plate 6, E); these coalesced to form necrotic areas (plate 6, F), and later the inoculated leaves became dry.

CURLY TOP

Orange larkspur (*Delphinium nudicaule*), a native perennial delphinium occurring in California and Oregon, has been experimentally infected with curly top, and the virus was recovered and transferred to healthy sugar beets by previously noninfective beet leafhoppers with the method described by Freitag and Severin (1). Orange larkspur infected

with curly top failed to develop symptoms of the disease under greenhouse conditions.

During the past ten years, inquiries have been received from scientists, seed companies, nurserymen, and growers of delphinium in home gardens, as to whether the virus of curly top transmitted by the beet leafhopper, *Eutettix tenellus* (Baker) causes phyllody and virescence or greening of the flowers in delphinium. An attempt was made to infect one variety of delphinium with the virus of curly top by means of infective male beet leafhoppers. Five healthy Wrexham delphiniums grown from seeds were each exposed to lots of 20 infective leafhoppers. When one lot of insects died, another lot of 20 males was put in the cage, each plant being inoculated with from 2 to 4 lots of leafhoppers. Wrexham delphinium was an unfavorable food plant for the beet leafhopper; the males lived from 4 to 8 days on the seedlings. The five delphiniums were kept under observation for a period of 7 months, but no symptoms developed; and repeated efforts to recover the curly-top virus were failures. It is evident that Wrexham delphinium is immune to the virus of curly top.

During the following spring, five Wrexham delphiniums used as check or control plants were inoculated with the aster-yellows virus by the geminate leafhopper and typical symptoms of this disease developed.

SUMMARY

Perennial delphinium has been proved to be infected with tomato spotted wilt in nature. This disease ranks next to aster yellows as a serious disease in the central-coastal regions of California. Delphinium has been demonstrated to be naturally infected with a virus complex including spotted wilt and celery calico.

Varieties and hybrid delphiniums have been experimentally infected with common cucumber mosaic and western cucumber mosaic. The type of infection was systemic.

Delphiniums were experimentally infected with tobacco ringspot and ordinary tobacco mosaic. The type of infection was systemic with tobacco ringspot and local with ordinary tobacco mosaic.

Orange larkspur (*Delphinium nudicaule*), a native perennial delphinium, has been reported in a previous paper (1) to be a symptomless carrier of curly top. Wrexham delphinium was immune to the virus of curly top.

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PLATES

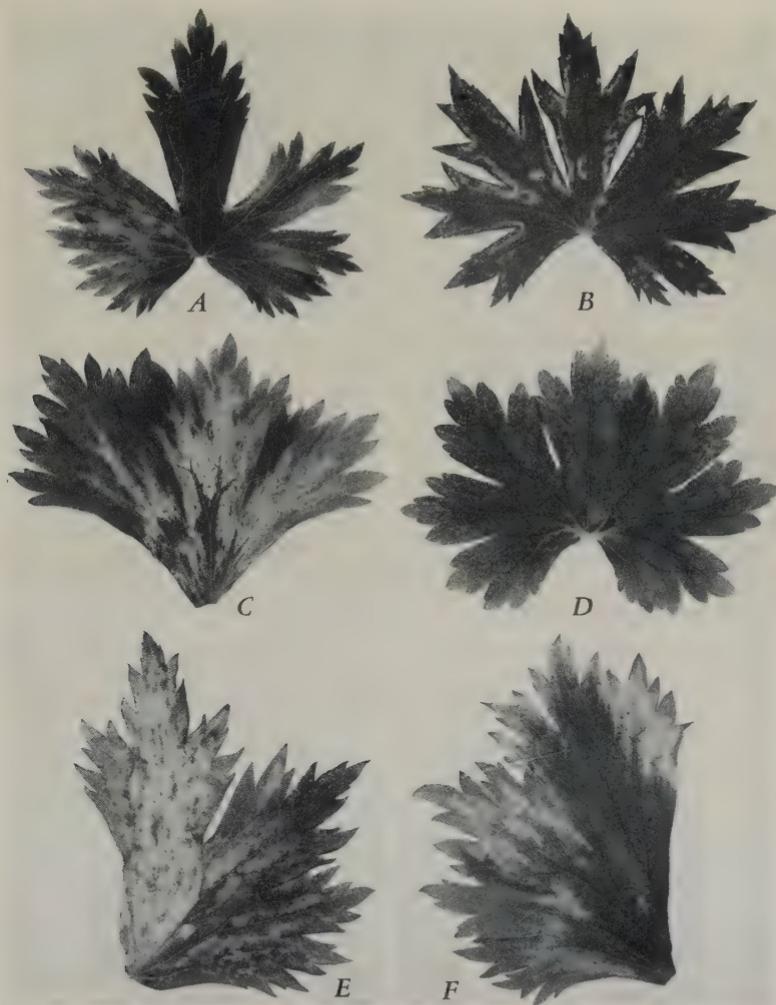


Plate 1.—Early stages of spotted wilt on leaves of delphiniums: *A*, pale-green areas, the first symptom of the disease; *B*, chlorotic rings surrounding green areas and broken, yellow bands along the margin; *C*, green or chlorotic banding of the veins and veinlets; *D*, *E*, double concentric rings of various sizes, each composed of an outer green and inner chlorotic ring, or a chlorotic ring encircling a green center; *F*, lemon-yellow discolorations along the margin and irregular, chlorotic areas.



Plate 2.—Late stages of spotted wilt on leaves of delphinium: *A*, black, irregular areas bounding chlorotic tissue; *B*, small pinpoint and large circular or irregular areas which frequently coalesce; *C, D*, black areas spreading in lobes; *E*, black region surrounding a ring that encloses a chlorotic center, and necrosis of veins and petioles; *F*, left lobes turning brown and becoming dry, and black areas on other lobes.

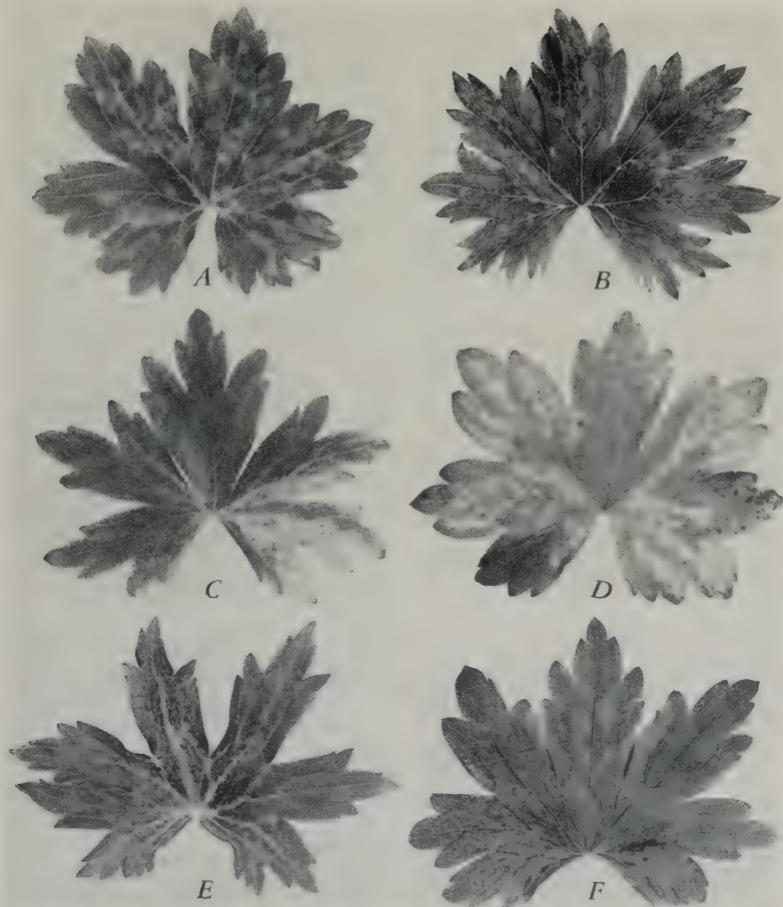


Plate 3.—Comparison of symptoms on the leaves of delphiniums infected with common cucumber mosaic (*A, C, E*) and with western cucumber mosaic (*B, D, F*): *A, B*, circular or elongated, chlorotic areas; *C, D*, green spotting in chlorotic areas; *E, F*, green vein banding.

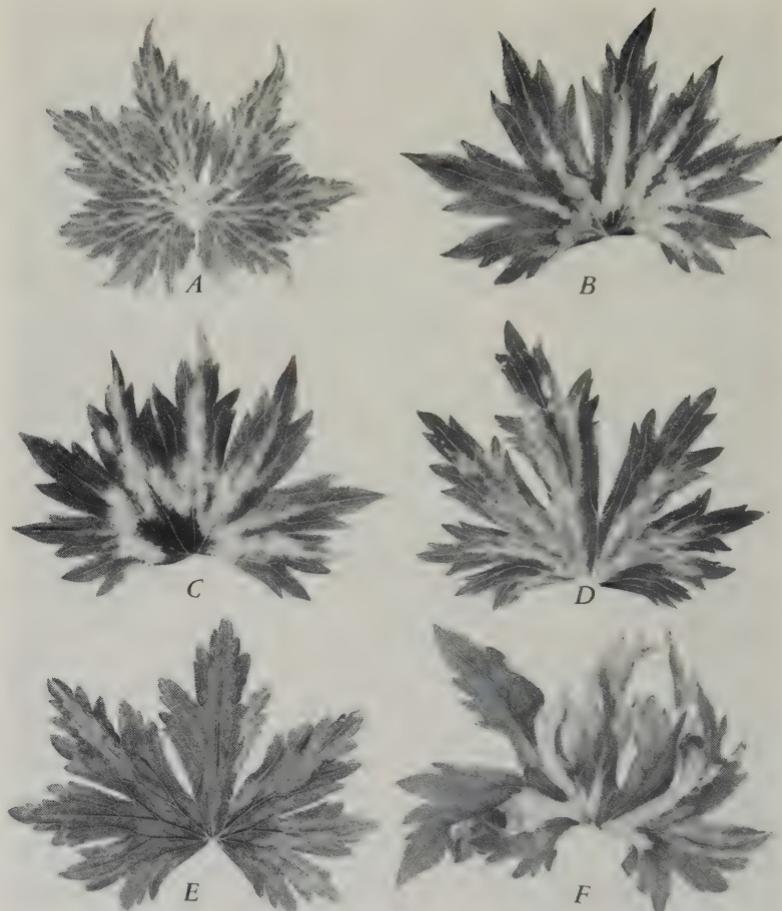


Plate 4.—Common-cucumber-mosaic symptoms on leaves of delphiniums: A, circular chlorotic areas distributed along the veins; B, pale-yellow vein banding; C, D, chlorosis spreading in all lobes; E, faint mottling or mosaic pattern; F, distortion, chlorosis, and blisterlike elevations.

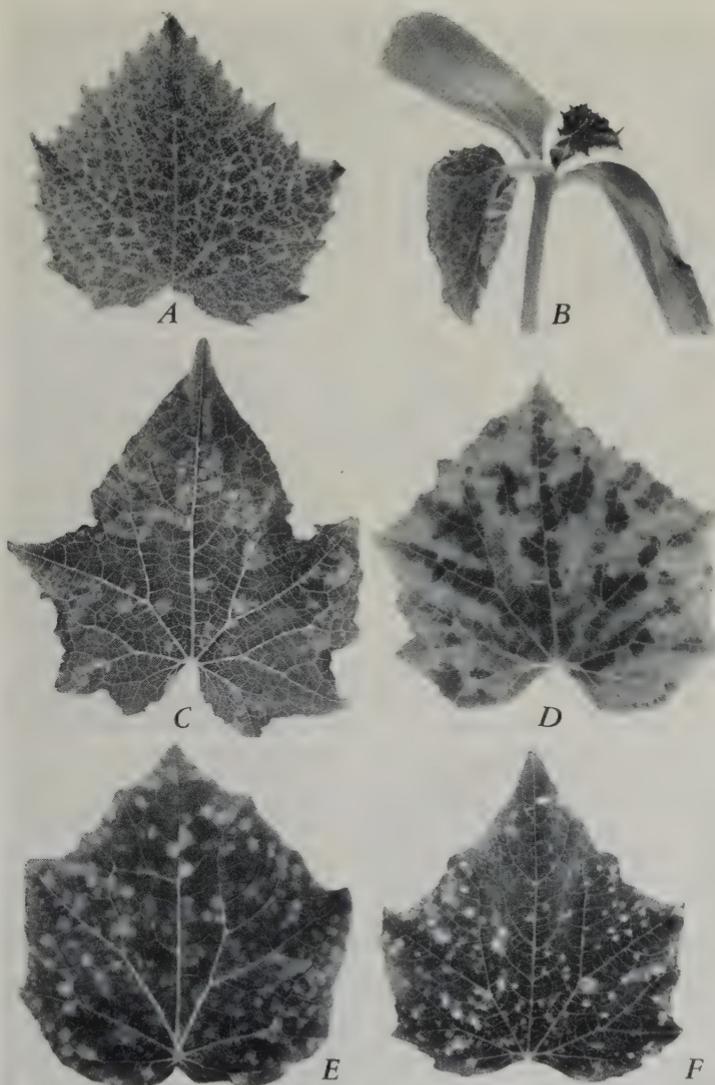


Plate 5.—Symptoms on leaves of White Spine cucumber (*Cucumis sativus*) produced by three viruses recovered from infected delphiniums: *A, B*, from seedlings infected with common cucumber mosaic, *A* showing cleared veinlets, and *B*, drooping of petiole and rolled margin of the first leaf and the balled second leaf; *C, D*, from plants infected with western cucumber mosaic, *C* showing small, circular, chlorotic areas on the first leaf, and *D*, chlorotic and green tissue forming a mottling; *E, F*, from plants infected with tobacco ringspot, *E* showing numerous, small, chlorotic areas, some bounded by cleared veinlets, and *F*, chlorotic rings with necrotic centers.

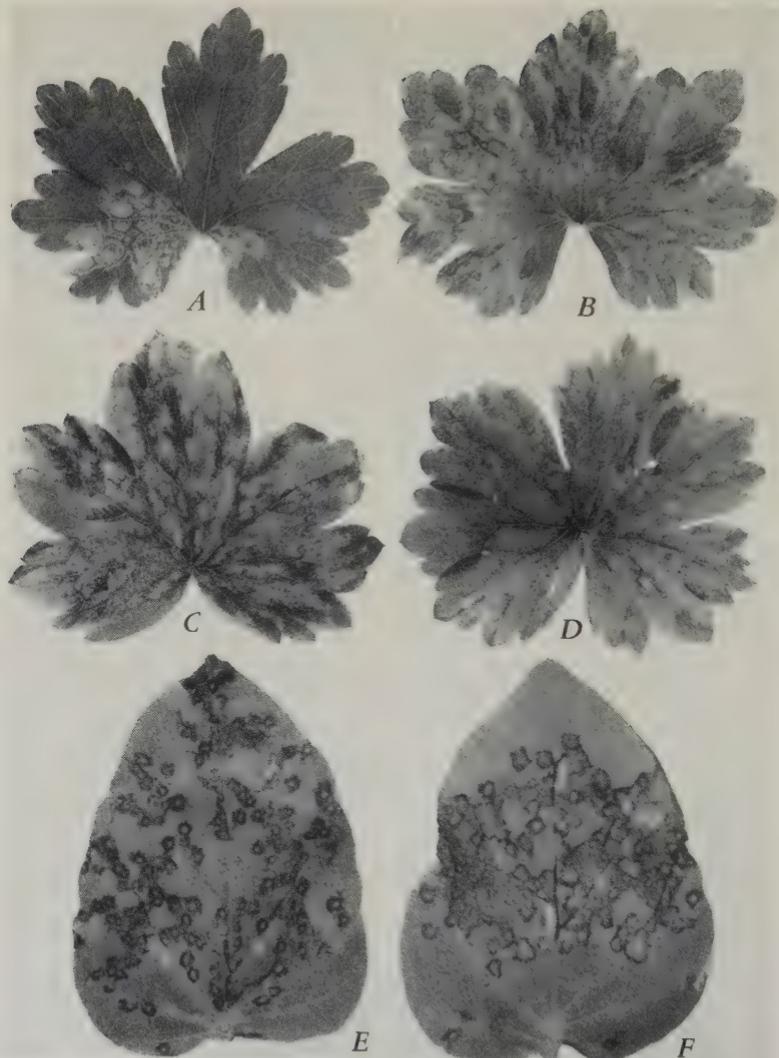


Plate 6.—*A, B*, Tobacco-ringspot symptoms on the leaves of delphinium seedlings: *A*, ringspots 5 weeks after inoculation, consisting of alternating concentric, chlorotic, and green rings surrounding either green or chlorotic tissue in the center; *B*, ringspots 8 weeks after inoculation, showing variation in size. *C, D*, Symptoms of ordinary tobacco mosaic on leaves of delphinium seedlings: *C*, brown necrotic streaks frequently on the veins of the inoculated leaf; *D*, interveinal, necrotic areas. *E, F*, Leaves of *Nicotiana glutinosa*: *E*, local lesions of ordinary-tobacco-mosaic virus which was recovered from infected delphiniums; *F*, local lesions coalescing to form necrotic areas.

LEAF VARIEGATIONS OF PERENNIAL
DELPHINIUMS

HENRY H. P. SEVERIN

LEAF VARIEGATIONS OF PERENNIAL DELPHINIUMS¹

HENRY H. P. SEVERIN²

LEAF VARIEGATIONS and variegations in flowers are not uncommon among ornamental flowering plants. In perennial delphiniums two types of leaf variegations, for which the names "golden-leaf" and "silver-leaf" variegations are proposed, have been observed in seedbeds, in cold frames covered with muslin, in commercial fields of delphiniums grown for seed production and for the cut-flower trade, in nurseries, and in home gardens.

Reichert (14)³ lists among diseases of ornamental plants in Palestine a nonparasitic yellow-leaf discoloration of *Delphinium* sp.

A leaf variegation somewhat similar to the leaf variegations of delphinium has become serious in certain strawberry varieties, affecting 25 to 50 per cent or all of the plants. The disease has been called "strawberry mosaic" (1), "suspected strawberry mosaic" (2, 8), "noninfectious chlorosis" (4), "June yellows" (11), "yellows" (9, 10), and "gold leaf" (8); and at present the accepted name is "leaf variegation" (3, 5, 6, 7, 12).

Berkeley (1), Guba (8), Plakidas (11), and Demaree and Darrow (7) failed to transmit leaf variegation in strawberries by insects, sap inoculations, and grafting of diseased and healthy runners, and thus presented conclusive evidence that the disease is noninfectious and not caused by a virus.

Berkeley (2) was first to suggest that leaf variegation in strawberries was of genetic origin. Clark (4) expressed the opinion that the disease was caused by a gene mutation and was hereditary. The evidence as a result of breeding work, according to Demaree and Darrow (7), suggests a sporting or mutation, which has been considered in most instances as the appearance of a recessive character in somatic tissue; they state: "Evidence so far indicates that leaf variegation is not due to a single gene. Even if by selfing no yellow plants appear, this is by no means evidence that a complimentary gene for yellowing may not be in the variety."

In the investigation of leaf variegations on perennial delphinium, the patterns on seedlings and plants growing in the field were studied; attempts were made to reproduce the variegations on delphinium seedlings

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² Associate Entomologist in the Experiment Station.

³ Italic figures in parentheses refer to "Literature Cited" at the end of this paper.

by mechanical inoculation and by means of different species of aphids. Virus diseases in leaf-variegated plants were studied; and transmission of leaf variegations through the seeds was tested.

DESCRIPTION OF LEAF VARIEGATIONS

Golden-Leaf Variegation.—The patterns of golden-leaf variegation resemble those of calico on second-year or older delphiniums, but the two troubles can readily be distinguished in the field. Golden-leaf variegation affects all of the leaves on a plant, including the upper or apical leaves on the stalks (plate 2, A, B). The symptoms of calico are confined to the basal and intermediate leaves; the upper or apical leaves on the stalks remain green. The line and ring patterns characteristic of calico on the leaves of seedlings and perennial delphiniums described in one of the preceding papers (15) have never been observed on plants affected with golden-leaf variegation.

The most prominent and characteristic pattern of golden-leaf variegation on perennial delphiniums is the large yellow areas which extend into the lobes or divisions of the leaves (plate 1, A; plate 2, A). When the spike and all of the leaves are cut off and the plants are given a rest period during the winter, the new leaves on the shoots may show faint, pale-yellow streaks which gradually enlarge (plate 1, B) or the larger golden-yellow or pale-yellow and green areas appear immediately instead of developing from the streaks. The early stages of leaf variegation on some plants may show yellow streaks (plate 1, C). Later the leaves lose more and more of their green color and become mottled with yellow and green (plate 1, D, E). The patterns vary considerably on perennial delphiniums; some show mostly streaking of the leaves (plate 2, B); others chiefly mottling, or a combination of both; or mostly large golden-yellow and green areas. The flowers appear normal on perennial delphiniums showing golden-leaf variegations.

Golden-leaf variegation seems to be of a systemic nature, since the new shoots which develop from the roots after a rest period show symptoms on all leaves.

Silver-Leaf Variegation.—The appearance of silver-leaf variegation is similar to the patterns of golden-leaf type except that grayish white instead of golden-yellow areas occur on the lobes or divisions of the leaves (fig. 1). Frequently delphinium seedlings show grayish-white areas with numerous, small, green dots (plate 2, C), and sometimes the lobes of a leaf from the same plant are nearly albino with chains of dots extending along the veins (plate 2, D). The silver-leaf variegations are frequently found in seedbeds but are rarely found on perennial delphiniums grow-

ing in the field. Seedlings showing silver-leaf variegations were transplanted from seedbeds in pots and were kept under observation in a glasshouse. A few of the seedlings later developed the golden-leaf patterns, but others retained the silver-leaf patterns. A delphinium plant was found near Salinas with golden-leaf variegation confined to the

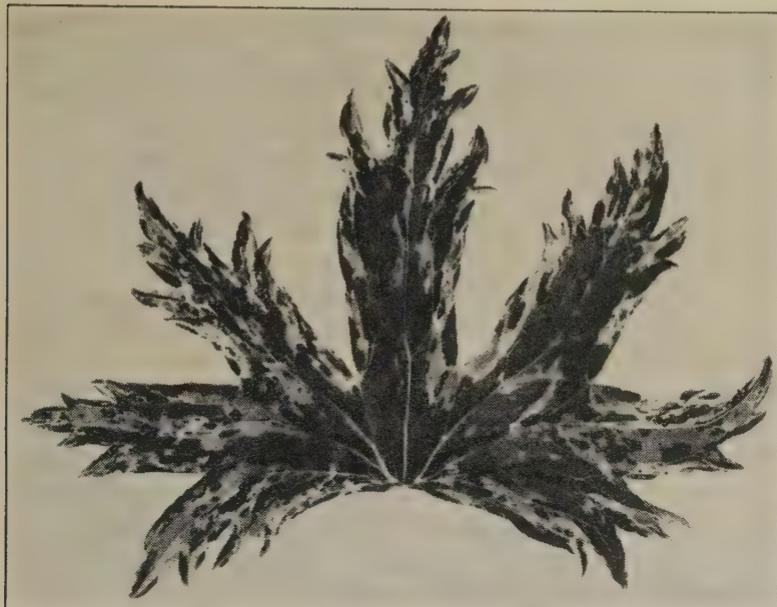


Fig. 1.—Delphinium leaf showing silver-leaf variegation with white or gray areas on the lobes.

basal and intermediate leaves and silver-leaf variegation to the upper leaves. Further investigations are necessary to determine whether the two types of leaf variegations are identical.

MECHANICAL INOCULATION

All attempts to transmit the causal agent of golden-leaf or silver-leaf variegation from 25 delphiniums by sap inoculation with the carborundum method (13) to healthy delphinium seedlings, Turkish tobacco, *Nicotiana glutinosa*, White Spine cucumbers, and celery, were failures.

APHIDS TESTED

The following ten species of aphids failed to transmit the causal agent of golden-leaf or silver-leaf variegations to healthy delphiniums:

Celery leaf aphid, *Aphis apigraveolens* Essig

Celery aphid, *Aphis apii* Theobald

- Rusty-banded aphid, *Aphis ferruginea-striata* Essig
Cotton, or melon, aphid, *Aphis gossypii* Glover
Erigeron root aphid, *Aphis middletonii* Thomas
Yellow willow aphid, *Cavariella capreae* (Fabricius)
Lily aphid, *Myzus circumflexus* (Buckton)
Foxglove aphid, *Myzus convolvuli* (Kaltenbach)
Green peach aphid, *Myzus persicae* (Sulzer)
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)

LEAF VARIEGATION, CALICO, AND ASTER YELLOWS

Delphinium plants may show leaf variegation and also harbor the calico virus. The juice was extracted from the leaves of two Dreer's De Luxe hybrid delphiniums showing golden-leaf variegation and inoculated in delphinium seedlings, Turkish tobacco, White Spine cucumbers, and celery. These host plants developed typical symptoms of calico, but leaf variegation failed to appear on the delphinium seedlings.

It was not uncommon to find delphinium plants under natural conditions showing both golden-leaf variegation and symptoms of aster yellows. The aster-yellows virus was recovered from Dreer's De Luxe hybrid delphiniums showing a combination of aster yellows and leaf variegation by previously noninfective long-winged aster leafhoppers, *Macrosteles divisus* (Uhl.); the mountain leafhopper, *Thamnotettix montanus* Van D.; and the geminate leafhopper, *T. geminatus* Van D.; and was transferred to healthy aster, celery, and delphinium plants; but leaf variegation again failed to appear.

Golden-leaf variegation is sometimes associated with both calico and aster yellows in the same plant under natural conditions. The inoculum from such plants produced symptoms of calico in Turkish tobacco, White Spine cucumber, celery, and delphinium, but not leaf variegation on delphinium seedlings. The aster-yellows virus was recovered by previously noninfective long-winged aster leafhoppers and transferred to healthy asters.

TRANSMISSION IN SEED

Golden-leaf and silver-leaf variegations were found among delphinium seedlings transplanted in cold frames covered with muslin; 1 per cent of the plants developed variegations before transplanting in the field. Many delphinium varieties and hybrids were grown from seeds in cages, and both types of leaf variegations appeared on the seedlings. Seeds were planted from one delphinium plant showing golden-leaf variegation, and all of the 18 seedlings developed this type of variegation. It is evident that the causal agent of leaf variegation is seed-borne.

On the other hand, in second-year Dreer's De Luxe hybrid delphin-

iums grown in the field, as high as 5 per cent of the plants were affected with leaf variegations. It may be possible that some delphinium seedlings develop leaf variegations after being transplanted in the field.

SUMMARY

Golden-leaf and silver-leaf variegations are nontransmissible by juice or insect inoculations and are seed-borne. They are not virus diseases.

ACKNOWLEDGMENTS

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PLATES

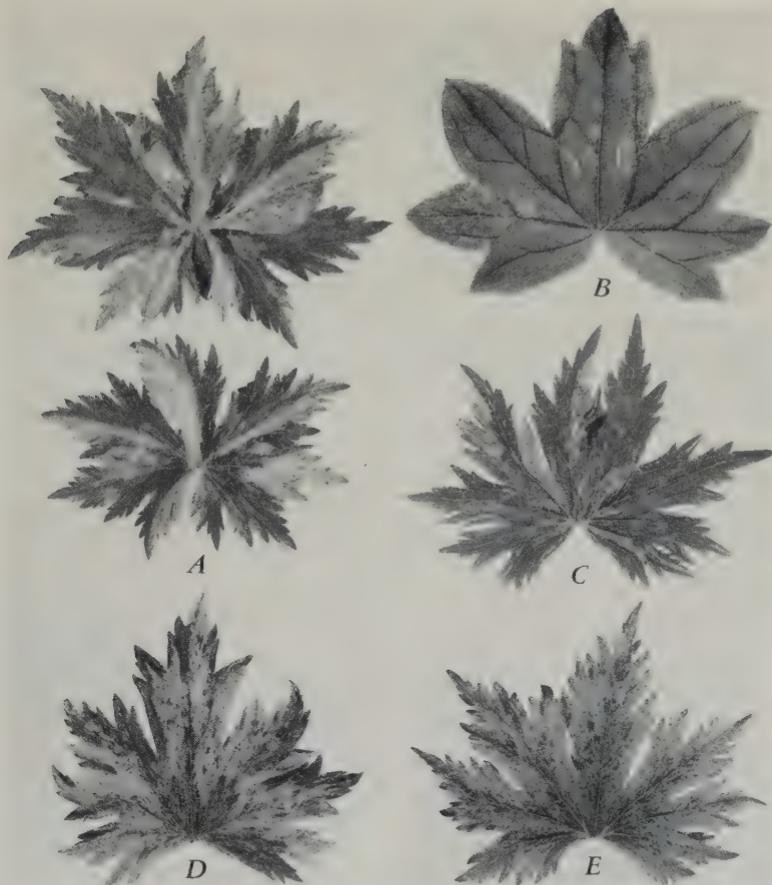


Plate 1.—Golden-leaf variegation from perennial delphiniums: *A*, large, yellow areas extending into the lobes or divisions of the leaves; *B*, faint, pale-yellow streaks on a leaf from a new shoot which grew from the roots after all of the leaves and the spike were cut off and the plant was given a rest period during the winter; *C*, yellow streaks; *D*, *E*, yellow and green mottling.



Plate 2.—*A*, *B*. Apical ends of delphinium shoots showing golden-leaf variegation; *C*, *D* two leaves from the same delphinium seedling showing silver-leaf variegations, with numerous, small, green dots scattered in the grayish-white lobes or arranged in chains along the veins.

VIROSES OF ANNUAL LARKSPURS

HENRY H. P. SEVERIN

VIROSES OF ANNUAL LARKSPURS¹

HENRY H. P. SEVERIN²

ANNUAL LARKSPURS are naturally infected with many virus diseases, in a few of which the identity of the virus has been determined. Annual and perennial larkspurs, or delphiniums, both belong to the genus *Delphinium*, and hence in connection with investigations of diseases and leaf variegations of perennial species (2, 3, 4, 5, 6)³ a study was undertaken to determine whether delphinium viroses (2, 3, 6) also affect annual species under natural conditions.

In this paper the following virus diseases of annual larkspurs are discussed: California aster yellows, celery calico, curly top, tomato spotted wilt, and western cucumber mosaic.

CALIFORNIA ASTER YELLOWS

Annual larkspur was demonstrated to be naturally infected with California aster yellows. The virus was recovered from naturally infected annual larkspurs grown for the cut-flower trade, in home gardens, and on seed farms. The virus was recovered from naturally infected annual larkspurs and transferred to asters by the short-winged and long-winged forms of aster leafhopper, *Macrostelus divisus* (Uhl.), and was transferred to celery by the mountain leafhopper, *Thamnotettix montanus* Van D., and by the geminate leafhopper, *T. geminatus* Van D.

Since short-winged and long-winged aster leafhoppers were not efficient vectors of the virus to perennial delphiniums and a high mortality occurred within 24 hours, an attempt was made to infect annual larkspurs with these leafhoppers experimentally. Table 1 gives a list of annual larkspurs which were infected with the virus. Both short-winged and long-winged aster leafhoppers infected 19 of the 24 plants inoculated, or 79.2 per cent. The virus was recovered from infected annual larkspurs by these leafhoppers and transferred to asters.

The longevity of short-winged aster leafhoppers on varieties of annual larkspur varied from 9 to 26 days for the males and from 15 to 22 days for the females; that of the long-winged aster leafhoppers varied from 8 to 13 days for the males and from 8 to 21 days for the females. Nymphs of both leafhoppers emerged from eggs deposited in larkspurs but none lived to become adults. The nymphal stages of the mountain and gemi-

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² Associate Entomologist in the Experiment Station.

³ Italic numbers in parentheses refer to "Literature Cited" at the end of this paper.

nate leafhoppers were completed on the Lilac Supreme, Sky Blue, Daintiness, and Exquisite Pink Improved varieties of annual larkspur.

The first symptom resulting from aster yellows on annual larkspur was a chlorotic appearance of the stem and flower stalk followed by a yellowing of the foliage. Droplets of clear sap sometimes exuded from the petioles and stems of experimentally infected annual larkspurs. Later the droplets turned brown and formed a crust, a symptom which also occurred on naturally infected larkspurs. Phyllody, or the tendency of the floral organs to resemble leafy structures, and virescence, or greening of the flowers, were somewhat similar to those described on perennial delphiniums in a previous paper (2). The sepals, petals, carpels, and stamens were often replaced by green leafy structures (plate 1, *B, F*) or the carpels were leaflike and the stamens were apparently normal (plate 1, *A, E*), and sometimes the carpels were replaced by stems bearing variously modified appendages frequently resembling leaves (plate 1, *C*).

The incubation period of the disease varied from 18 to 62 days, with an average of 36.4 days, as indicated in table 1.

CELERY CALICO

Annual larkspur was proved to be infected with celery calico in nature. The virus was recovered from naturally infected larkspurs and transferred by mechanical inoculation (1) to celery, Turkish tobacco, and White Spine cucumbers.

The varieties of larkspurs experimentally infected by mechanical inoculation are listed in table 2. A total of 108 annual larkspurs were inoculated, and 101, or 93.5 per cent, became infected, as shown in table 2. The virus was recovered and transferred to White Spine cucumber (table 2).

It is often difficult to detect symptoms of calico on the multifid linear segments of the leaves. Small green areas embedded in yellow portions of the leaves (plate 2, *D*) proved to be a reliable symptom of the disease.

CURLY TOP

Annual larkspurs have been demonstrated to be infected with curly top in the San Joaquin Valley. Previously noninfective beet leafhoppers, *Eutettix tenellus* (Baker), after feeding on the naturally infected plants, were transferred to sugar beets, and typical symptoms of the disease developed.

The following varieties of annual larkspurs were experimentally in-

fected with curly top by means of infective beet leafhoppers: Double mixed, Gloria, Exquisite Pink Improved, Lilac, Pink, and Sky Blue.

The method used to experimentally infect annual larkspurs grown from seeds was to allow 20 infective male beet leafhoppers to feed on

TABLE 1

TRANSMISSION OF CALIFORNIA-ASTER-YELLOW VIRUS BY SHORT-WINGED AND LONG-WINGED ASTER LEAFHOPPERS TO ANNUAL LARKSPURS AND
INCUBATION PERIOD OF THE DISEASE

Type and variety of annual larkspur	With short-winged aster leafhopper			With long-winged aster leafhopper			Incubation period of disease in plant, with both insects
	Plants inoculated	Period of inoculation	Plants infected	Plants inoculated	Period of inoculation	Plants infected	
	number	days	number	number	days	number	days
Giant Imperial Double:							
Carmine King.....	1	1	0	1	1	1	32
Daintiness.....	2	20, 26	2	2	13, 20	1
Double mixed.....	1	13	1	1	13	1
Exquisite Pink Improved	2	10, 15	2	2	2, 8	1
Gloria.....	2	16, 22	2	2	8, 21	1
La France.....	1	2	1	1	2	1
Lilac Spire.....	1	1	1	1	1	1	45, 61
Miss California.....	1	1	1	1	1	1	35, 35
White King.....	1	1	0	1	1	1	25
White Spire.....	1	1	1	1	1	1	34, 34
Tall Double Stock-flowered:							
Bright Rose.....	1	1	1	1	1	1	28, 28
Bright Violet.....	1	1	0	1	1	1	30
Dark Blue.....	1	1	1	1	1	0	47
Lilac.....	1	1	1	1	1	1	18, 27
Lilac Supreme.....	2	18, 7	2	2	9, 9	1
Lustrous Carmine.....	1	1	0	1	1	1	62
Pink.....	1	14	1	1	9	1
Sky Blue.....	2	9, 18	2	2	9, 11	2
White.....	1	1	0	1	1	1	42
Total or average.....	24	19	24	19	36.4

each plant for a period varying from 1 to 14 days. Males were used rather than females to avoid egg deposition. The leafhoppers were then removed from the inoculated plants and played no further part in the experiment.

The method used to recover the virus from larkspurs after symptoms appeared was to feed lots of 20 previously noninfective males on each infected plant for a period of 3 days, then healthy sugar beets were exposed to the leafhoppers until symptoms of the disease developed.

Annual larkspurs infected with curly-top virus were stunted with bunched leaves at the apical end of the stem and on the axillary shoots

TABLE 2

LIST OF ANNUAL LARKSPURS EXPERIMENTALLY INFECTED WITH CELERY CALICO AND WESTERN CUCUMBER MOSAIC AND RECOVERY OF VIRUSES

Type and variety of annual larkspur	Celery calico				Western cucumber mosaic			
	Larkspurs inoculated	Larkspurs infected	Recovery of virus from infected larkspurs		Larkspurs inoculated	Larkspurs infected	Recovery of virus from infected larkspurs	
			Cucumbers inoculated	Cucumbers infected			Cucumbers inoculated	Cucumbers infected
	number	number	number	number	number	number	number	number
Giant Imperial Double:								
Blue Bell.....	3	2	10	2	5	3	25	12
Blue Spire.....	8	8	40	40	8	6	40	26
Carmine King....	13	13	65	65	5	5	25	25
Coral King.....	3	3	15	3	3	3	15	15
Daintiness.....	6	6	30	30	5	5	25	25
Mixed.....	3	1	5	1	3	3	15	12
Exquisite Pink Improved.....	1	1	5	5	4	4	20	20
Exquisite Rose.....	7	6	30	30	5	5	25	25
Gloria.....	4	4	20	17	6	6	30	30
Hyacinth.....	5	5	25	25	5	5	25	25
La France.....	3	3	15	15	3	3	15	15
Lilac Spire.....	3	3	15	12	6	6	30	18
Los Angeles Improved.....	3	3	15	15	3	2	15	2
Miss California.....	3	3	15	15	3	3	15	3
White King.....	3	3	15	12	3	3	15	15
White Spire.....	3	3	15	15	3	3	15	3
Tall Double Stock-flowered:								
Bright Rose.....	3	3	15	15	3	3	15	3
Bright Violet.....	3	2	10	4	3	3	15	15
Dark Blue.....	3	1	5	1	3	3	15	15
Mixed.....	6	6	30	30	5	5	25	25
Lilac.....	5	5	25	25	5	5	25	25
Lilac Supreme.....	1	1	5	5	5	5	25	25
Lustrous Carmine.....	3	3	15	15	3	3	15	15
Pink.....	1	1	5	5	3	3	15	15
Rosamond.....	5	5	25	25	5	5	25	25
Rosy Scarlet.....	3	3	15	9	3	3	15	15
Sky Blue.....	1	1	5	5	5	2	25	2
White.....	3	3	15	15	3	3	15	9
Total.....	108	101	505	456	116	108	550	460
Percentage....	..	93.5	..	90.3	..	93.1	..	89.6

arising from the nodes and with the lower and intermediate leaves downwardly curled (plate 2, C).

The incubation period of the disease varied from 22 to 33 days.

TOMATO SPOTTED WILT

Annual larkspurs frequently have been observed with black leaves under natural conditions indicating an infection of tomato spotted wilt. No attempt has been made to recover the virus from such plants nor to infect healthy plants experimentally.

WESTERN CUCUMBER MOSAIC

Annual larkspurs have not been found to be infected with western cucumber mosaic in the central-coastal regions of California, but no plants have been tested from the Sacramento and San Joaquin valleys, where the virus is known to occur.

A list of varieties of larkspurs experimentally infected by mechanical inoculation (1) is shown in table 2. A total of 116 annual larkspurs were inoculated, and 108, or 93.1 per cent, became infected, as shown in table 2. The virus was recovered from infected plants and transferred to White Spine cucumbers (table 2).

It is often difficult to detect visible symptoms of the disease on the linear segments of the leaves, but under the binocular microscope a mottling appears, consisting of elliptical, circular, or irregular chlorotic areas which coalesce later and form elongated streaks. The multifid segments of the leaves are sometimes malformed (plate 2, B). When larkspurs are severely affected by the disease, the plants are stunted and the leaves are bunched around the stem (plate 2, A). A cluster of abnormal, dwarfed flowers develops on the apical end of the stem of stunted plants but no breaking in color occurs.

SUMMARY

Annual larkspurs have been demonstrated to be naturally infected with California aster yellows, celery calico, and curly top. They have been experimentally infected with western cucumber mosaic.

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PLATES

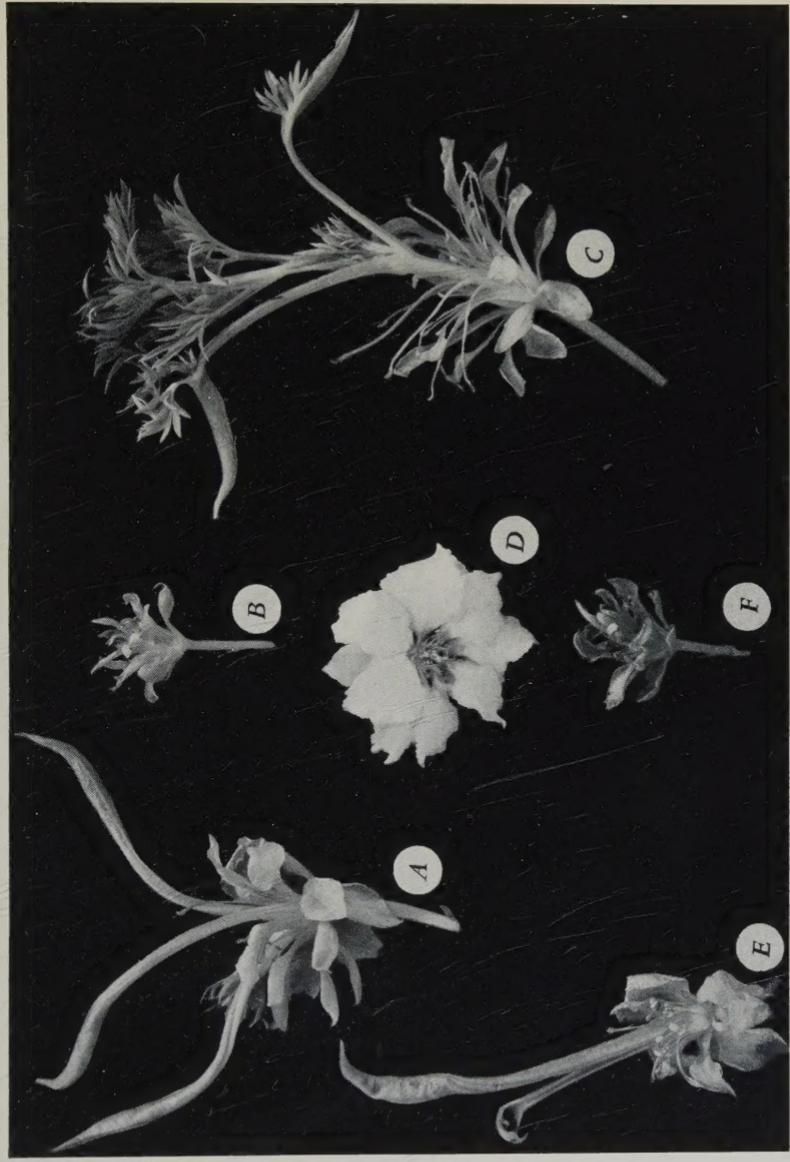


Plate 1.—Center, *D*, flower from healthy annual larkspur, others from plants infected with California aster yellows, showing phyllody and virensce; *A*, *E*, carpels leaflike, stamens apparently normal; *B*, *F*, sepals, petals, carpels, and stamens replaced by green leafy structures; *C*, carpels replaced by stems bearing variously modified appendages resembling leaves.



Plate 2.—*A, B*, Annual larkspur experimentally infected with western cucumber mosaic; *A*, entire plant stunted, with leaves bunched around the stem; *B*, malformed leaves. *C*, Annual larkspur experimentally infected with curly top showing dwarfing of entire plant with bunched leaves at the apical end of the stem and on the axillary shoots arising from the nodes, and with lower and intermediate leaves downwardly curled. *D*, Leaves from annual larkspur experimentally infected with celery calico showing green areas embedded in the yellow portions of the blades.